

A REVISION OF THE SHORE-FLY GENUS *LEMNAPHILA* CRESSON (DIPTERA: EPHYDRIDAE)

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Abstract.—Species of the shore-fly genus *Lemnaphila* Cresson are revised, including the description of two new species: *L. grossoae* (Argentina. Tucumán: San Miguel de Tucumán) and *L. longicera* (Peru. Loreto: Iquitos). *Lemnaphila* is known thus far only from the New World, where there are now five species. All species with known biologies are miners in various species of Lemnaceae. Although *Lemnaphila* is clearly a monophyletic clade based on several synapomorphies, its relationship to other genera of the tribe Hydrelliini is unresolved.

Key Words: Revision, Diptera, Ephydridae, shore flies, *Lemnaphila*, *L. longicera*, *L. grossoae*, New World

Specimens of *Lemnaphila* Cresson are among the smallest shore flies, with adult flies often being less than one mm in length. Their small size corresponds well with, and is apparently an adaptation to, the mining behavior of the larval instars in the tiny thalli of the duckweed family Lemnaceae, especially the genus *Lemna* L. Their small size evidently has been a deterrent to their study, as specimens are seldom collected and are poorly represented in collections, and very few studies that concern the genus have been published. Duckweed, moreover, is often an overlooked component of aquatic environments, and studies pertaining to the rearing and identification of phytophagous insects associated with species of Lemnaceae are uncommon (Scotland 1940, Buckingham 1989). Our experience in the field, however, indicates that specimens of *Lemnaphila* are frequently numerous when the duckweed habitat is adequately sam-

pled. Indeed, recent collecting has revealed a fifth species from Peru, a sixth species from Argentina, and also major extensions in the distributions of the other species. Additional studies on their natural history, including fresh larval and puparial material of *L. scotlandae* Cresson, were conducted in Ohio. Describing and documenting these discoveries are the primary objectives for this revision. Further information on the natural history of *L. scotlandae* will be published separately (Edmiston and Foote, in preparation).

Cresson (1933) first described *Lemnaphila* as a monotypic genus, being known only from *L. scotlandae* Cresson. Miss Minnie B. Scotland, after whom this species was named, discovered the rather minute adults of *L. scotlandae* on *Lemna* that was growing in a fish hatchery in Ithaca, New York. Miss Scotland conducted studies on this species and published three papers

(1934, 1939, 1940) on its natural history. The genus remained monotypic until Lizarralde de Grosso (1977, 1978) described three additional species, all based on specimens collected in the neotropics. In the first paper, Lizarralde de Grosso (1977) described two of the new species: *L. neotropica* (Argentina (La Plata), Panama, and Jamaica) and *L. wirthi* (Ecuador). Lizarralde de Grosso (1978) described the third species, *L. lilloana*, from specimens collected in Argentina (Tucumán). In the second paper, she also described the immature stages of *L. lilloana* and *L. neotropica* and reported the occurrence of *L. wirthi* in Argentina (Tucumán). Lizarralde de Grosso (1980) published a third paper in which the larvae of *Lemnaphila* are distinguished from other shore flies.

Other than catalog entries (Wirth 1965, Mathis and Zatwarnicki 1995), new state records (Deonier and Regensburg 1978, Steinly et al. 1987), and records of parasitoids (Marsh 1979, Muesebeck 1979), few published records on *Lemnaphila* are available. Johannsen (1935) included *Lemnaphila* in his generic key to the immature stages of shore flies, as did Courtney et al. (1996) and Merritt et al. (1996). The latter two papers also summarized known information on the biology of the larvae. Wirth and Stone (1956) and Wirth et al. (1987) included *Lemnaphila* in their keys to the shore-fly genera of the Nearctic Region. In a synopsis of shore-fly biology, Foote (1995) also reviewed the biology of *Lemnaphila*.

The descriptive terminology, with the exceptions noted in Mathis (1986) and Mathis and Zatwarnicki (1990a), follows that published in the *Manual of Nearctic Diptera* (McAlpine 1981). Because specimens are small, usually less than 3.5 mm in length, study and illustration of the male terminalia required use of a compound microscope. Although we followed the terminology for most structures of the male terminalia that other workers in Ephydriidae have used (see references in Mathis 1986; Mathis and Za-

twarnicki 1990a, 1990b), Zatwarnicki (1996) now uses alternative terms (medandrium, transandrium) that are based on the "hinge" hypothesis for the origin of the eremoneuran hypopygium. The terminology for structures of the male terminalia is provided directly on Figs. 4–6 and is not repeated for comparable illustrations of other species.

Dissections of male genitalia were performed using the method of Clausen and Cook (1971) and Grimaldi (1987). External morphology and internal genitalic features were drawn using a drawing tube on a Wild M20EB compound and a M5 dissecting microscope. The species descriptions are composite and are not based solely on the holotypes. Two head and two venational ratios used in the descriptions are defined below (all ratios are based on measurements from a minimum of five specimens). All measurements were made from pinned specimens.

Eye ratio is the eye width divided by the eye height.

Gena-to-eye ratio is the genal height measured at the maximum eye height divided by the eye height.

Costal vein ratio is the straight line distance between the apices of R_{2+3} and R_{4+5} /distance between the apices of R_1 and R_{2+3} .

M vein ratio is the straight line distance along vein M between crossveins (dm-cu and r-m)/distance apicad of dm-cu.

The phylogenetic analysis was performed with the assistance of Hennig86©, a computerized algorithm that produces cladograms by parsimony. Before analysis, character data were arranged in transformation series and then polarized, primarily using outgroup procedures.

Rearing.—All field and laboratory work was carried out in northeastern Ohio near the city of Kent in Portage County. Laboratory rearings, providing life cycle data, were carried out in an environmental chamber programmed to give a photoperiod of 16L:8D and a temperature variation between 22–32° C. Adults were collected

from a marsh near the Kent State University stadium and placed in plastic tumblers with approximately 100 ml of pond water. *Lemna* thalli (approximately 25) were placed in each tumbler. The tumbler was covered with cheese cloth held in place by a rubber band.

Immature descriptions.—Specimens collected from the field or reared in the laboratory were preserved in 70% ethanol or double mounted and dried. External and internal morphologic structures were drawn using an ocular grid on a Zeiss compound microscope. Continuous characters were measured using a calibrated ocular micrometer attached to a Zeiss compound microscope. Descriptive terminology of immature stages follows McAlpine (1981). The tentoropharyngeal sclerite length and width are the maximum straight line distances in lateral view from the anterior tip to the dorsal cornu posterior tip (A-PDC), from the anterior tip to the ventral cornu posterior tip (A-VDC), and from the dorsal cornu posterior tip to the ventral cornu posterior tip (PDC-VDC).

Fecundity.—Females collected from the field were isolated in individual tumblers. The number of eggs laid on *Lemna* thalli were counted on each of four days. Each day, the female was removed from the tumbler and placed in a fresh preparation with 25 new *Lemna* thalli.

Life History.—Eggs deposited on the *Lemna* thalli were placed individually in 20 ml plastic vials. Eggs were observed each day for hatching, and individual flies were observed each day for molting between instars, pupariation, and adult emergence.

Specimens.—Although most specimens for this study are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), we also studied numerous specimens that are deposited in the American Museum of Natural History (AMNH), New York; the Academy of Natural Sciences of Philadelphia (ANSP), Pennsylvania; The Natural History Museum (BMNH), London, England; Canadian

National Collection (CNC), Ottawa, Ontario; Cornell University (CU), Ithaca, New York; Guelph University (GUE), Guelph, Ontario; personal collection of James F. Edmiston (JEPC); Instituto Miguel Lillo (IML), Tucumán, Argentina; Ohio State University (OHSU), Columbus; Universidad de La Plata, La Plata, Argentina (UNLP) and Washington State University (WSU).

SYSTEMATICS

We follow Deonier's (1995) tribal characterization of Hydrelliini and the generic composition of the tribe that Mathis and Zatzwornicki (1995) published. Deonier (1995) published a key to the three genera, including *Cavatorella*, which he described in the same paper. Deonier's concept of *Lemnaphila*, as reflected in the key, was based primarily on *L. scotlandae*, the type species, but with the addition of other species, the characterization of the genus has been adjusted as indicated in the following revised key to genera.

KEY TO GENERA OF HYDRELLIINI ROBINEAU-DESVOIDY

(modified from Deonier 1995)

1. Posterior notopleural seta inserted near dorsal angle; prescutellar acrostichal seta lacking; ocellar setae lacking; anepisternum bearing a single seta along posterior margin; lacking an intrapostalar setula *Lemnaphila* Cresson
- Posterior notopleural seta inserted at same level as anterior seta near ventral margin; prescutellar acrostichal seta present; ocellar setae usually present; anepisternum usually bearing 1 large seta and 1-2 smaller setae along posterior margin; usually bearing 1 intrapostalar setula 2
2. Wing apex broadly rounded; vein R_{2+3} long, making costal section II much longer than section III; interfacetal setulae conspicuous and dense; male lacking ventroclinate processes from dorsad of fused surstyli *Hydrellia* Robineau-Desvoidy
- Wing apex narrowly rounded, ellipsoidal; vein R_{2+3} short, making costal section II subequal to section III; costa bearing several interfacetal setae; interfacetal setulae inconspicuous, sparse; male with ventroclinate styliform pro-

cesses projected from dorsad of fused surstyli
..... *Cavatorella* Deonier

Genus *Lemnaphila* Cresson

Lemnaphila Cresson, 1933:229. Type species: *Lemnaphila scotlandae* Cresson, 1933, monotypy; 1944:175–176 [review, tribal relationships].—Scotland, 1934:291 [biology, larval miner in *Lemna*]; 1939:713–718 [biology, parasatoids]; 1940:322–324 [review of biology, figs. of egg, puparium, adults].—Johanssen, 1935:48–51 [larval key].—Wirth, 1965:745 [Nearctic catalog].—Wirth and Stone, 1956:465, 469 [key to genus, leaf mining habit].—Lizarralde de Grosso, 1977:159–164 [review]; 1980:55–60 [larval key]; 1989:54–55 [review, Argentina fauna].—Wirth et al., 1987:1035, 1041 [fig. of head, key to genus].—Mathis and Zatzwornicki, 1995:96–97 [world catalog].—Courtney et al., 1996:508 [larval key to genus].—Merritt et al., 1996:545 [habitat, habits, trophic relationships].

Diagnosis.—*Lemnaphila* is a genus of the tribe Hydrelliini, subfamily Hydrelliinae, that is similar and closely related to *Hydrellia* Robineau-Desvoidy and *Cavatorella*. *Lemnaphila*, which are minute to small shore flies (length 0.83–1.50 mm), is distinguished from these and other shore-fly genera by the following combination of characters:

Head: Frons much wider than long, sometimes with distinct mesofrons and parafrons; mesofrons broadly reaching anterior margin of frons, vestiture variable. Ocellar and paraverticlar setae lacking; pseudopostocellar setae well developed, proclinate and slightly divergent. Pedicel lacking a large, dorsoapical seta; arista with 5–9 long rays along dorsum. Face in lateral view vertically straight or shallowly concave and with ventral third slightly angled anteriorly; ventral facial margin at most shallowly arched; facial seta 1 near ventrolateral margin, sometimes with a few setulae, generally weakly developed. Eye comparatively large, especially in lateral view, bearing nu-

merous interfacetal setulae. Gena very short, gena-to-eye ratio less than 0.15; lacking a prominent genal seta. Clypeus not generally exposed.

Thorax: Chaetotaxy: dorsocentral setae 2 (0+2 or with anterior seta on transverse suture), posterior dorsocentral seta displaced laterally (this seta has sometimes been labeled as the intra-alar seta); lacking prescutellar acrostichal setae, other acrostichal setae variable, either lacking or with a few setulae in 2 anterior rows; presutural supra-alar seta present but often reduced; lacking postpronotal, postsutural supra-alar, and intrapostalar setae; 1 postalar seta; 2 lateral scutellar setae (lacking a smaller setula between 2 larger setae), basal seta shorter than apical seta; 2 notopleural setae, anterior seta usually shorter, posterior seta inserted near dorsal angle of notopleuron; 1 anepisternal seta along posterior margin; kataposternal seta variable, lacking, reduced, or well developed. Wing: generally hyaline or very faintly infuscate; costal vein long, extended to vein M; vein R_{2+3} short, with costal section II equal to section II or much shorter than section III; lacking greatly elongate interfractural setulae other than apical seta. Legs lacking dorsoerect setae on dorsal surface.

Abdomen: Dorsum comprising tergites 1–5, with tergites 1–2 somewhat fused; sternite 1 greatly reduced or lacking, 2–5 present; 5th sternite of male comparatively well developed and much larger than sternites 2–4, bearing setulae, shape variable with species. Male terminalia: Epandrium weakly developed, incomplete dorsally with a membranous gap between lateral extensions, lateral extensions as a fused lateral phalange at base of cerci; cerci well developed, fused with median margin of epandrium; surstylus greatly reduced as a small, usually narrow process from ventral margin of fused epandrium/cerci; subepandrial plate well developed, simple, arched; aedeagus well developed, sometimes angulate in lateral view; aedeagal apodeme narrow to very broadly developed, keel variously

developed, usually enlarged; postgonite well developed, usually bearing setulae near midlength; pregonite apparently lacking; hypandrium simple, lateral apices oriented posteriorly, shallowly arched or narrowly V-shaped.

Discussion.—As noted in the generic diagnosis, we place *Lemnaphila* in the tribe Hydrelliini, subfamily Hydrelliinae, where it is closely related to *Hydrellia* and *Cavatorella*. Although this tribal assignment and the generic associations are now apparent, these relationships were not always recognized and there was some confusion that led to a rather circular history. When Cresson (1933) described *Lemnaphila* he placed the genus “. . . in the tribe Hydrelliae of the subfamily Notiphilinae, near the genus *Nostima*.” Cresson based his generic placement on adult characters (setulose eyes, antennal shape, and the arrangement and number of dorsocentral setae). Cresson (1944), however, then removed *Nostima* Coquillett, *Philygria* Stenhammar, and *Lemnaphila* from the tribe Hydrelliini and created a new tribe, Hydrinini (unavailable, based on a junior homonym, = Philygriini Lizarralde de Grosso), for these three genera. Despite removing *Lemnaphila* from a close association with *Hydrellia*, Cresson (1944:176) continued to recognize that *Lemnaphila* has “. . . the appearance of a small *Hydrellia*.” The tribe Philygriini was then characterized primarily by the elevated insertion of the posterior notopleural seta and the reduced setation. Wirth (1965) followed Cresson's suprageneric arrangement for the Tribe Philygriini in his catalog of North American Ephydriidae. Dahl (1959), in his review of Scandinavian Ephydriidae, removed *Nostima* and *Philygria* from the subfamily Notiphilinae (= Hydrelliinae) and placed these genera along with *Hyadina* Haliday in the subfamily “Hydrininae” (unavailable, based on a junior homonym, = Ilytheinae Cresson), which Dahl described in the same paper. Mathis and Zatwarnicki (1990b) also recognized Philygriini but with only two genera: *Philygria* and

Nostima. They suggested that *Lemnaphila* was better placed in the tribe Hydrelliini (Subfamily Hydrelliinae) near the genus *Hydrellia* based especially on characters of the male terminalia and larvae, and in subsequent publications (Zatwarnicki 1992, Deonier 1995, and Mathis and Zatwarnicki 1995), *Lemnaphila* was placed in the Hydrelliini, along with *Hydrellia* and *Cavatorella*.

Cresson (1933, 1944) first noted that adults of *Lemnaphila* are similar to *Hydrellia*, and a close relationship between these two genera is strongly supported by larval characters as well. Johannsen (1935) was able to distinguish between larvae of *Lemnaphila* and *Hydrellia* only on the basis of larval size and the preference *Lemnaphila* has for feeding on *Lemna*. *Hydrellia* is generally characterized by its stem- and leaf-mining habits, and Johannsen observed that the mouthparts of *Lemnaphila* and *Hydrellia* were identical except for size. Hennig (1943) also proposed a close relationship between larvae of *Lemnaphila* and *Hydrellia*. Lizarralde de Grosso (1977, 1978) described additional Neotropical species of *Lemnaphila*, including larval descriptions, and indicated that the Neotropical larvae of *Hydrellia* and *Lemnaphila* are very similar and closely related.

Specimens of *Lemnaphila* are not only tiny but they are highly derived, in part and presumably as an adaptation to the mining habit in Lemnaceae. The structures of the male terminalia also reflect their derived condition. The surstylus, for example, is highly modified as a much reduced structure at the ventral margin of the fused epandrium/cercus. The reduced epandrium that is fused to the cercus and the enlarged cerci are also evidence of the derived status.

KEY TO SPECIES OF *LEMNAPHILA* CRESSON

1. Scape, pedicel, and basal half of 1st flagellomere yellow; length of 1st flagellomere twice its height; face in profile straight; length of outer vertical seta less than half length of inner vertical seta. Katepisternum whitish yellow, concolorous with forecoxa

- *L. longicera*, new species
- Antenna entirely dark brown; length of 1st flagellomere only slightly longer than its height; face shallowly concave in lateral view with ventral third slightly angled forward; length of outer vertical seta about 3/4 length of inner vertical seta. Katepisternum brown 2
- 2. Fronto-orbital setulae greatly reduced, at most hairlike, none well developed; mesofrons subshiny, distinct from densely microtomentose parafrons. Scutellum lacking microtomentum or sparsely microtomentose, not appearing velvety; katepisternal seta reduced, hairlike
..... *L. scotlandae* Cresson
- At least 1 fronto-orbital seta well developed, anterior setula proclinate, posterior seta much longer, length subequal to outer vertical seta, laterocline, parallel to outer vertical seta; mesofrons and parafrons densely microtomentose, appearing velvety, or with small area immediately anterior of ocellar triangle bare (*L. lil-loana*), shiny. Scutellum moderately to densely microtomentose, brownish black to black, sometimes appearing velvety; katepisternal seta well developed, length subequal to posterior anepisternal seta 3
- 3. Ventral third of face densely microtomentose, blackish brown, concolorous with dorsal portion of face; coxae, femora, and tibiae yellow
..... *L. wirthi* Lizarralde de Grosso
- Ventral third of face densely microtomentose, silvery white, distinctly contrasted with blackish brown dorsal portion; femora brown, otherwise legs yellow 4
- 4. Area immediately laterad and antiad of ocellar triangle silvery white, concolorous with fronto-orbit immediately anterior and posterior of laterocline fronto-orbital seta
..... *L. grossoae*, new species
- Area immediately laterad and antiad of ocellar triangle dark brown, similar to coloration of ocellar triangle 5
- 5. Mesofrons and parafrons densely microtomentose, appearing velvety blackish brown; posterior fronto-orbit extensively white to silvery white
..... *L. neotropica* Lizarralde de Grosso
- Mesofrons just anterior of ocellar triangle bare, shiny, blackish brown, contrasted with densely microtomentose parafrons; posterior fronto-orbit with very small area white
..... *L. lilloana* Lizarralde de Grosso

***Lemnaphila longicera* Mathis and
Edmiston, new species**
(Figs. 1–3)

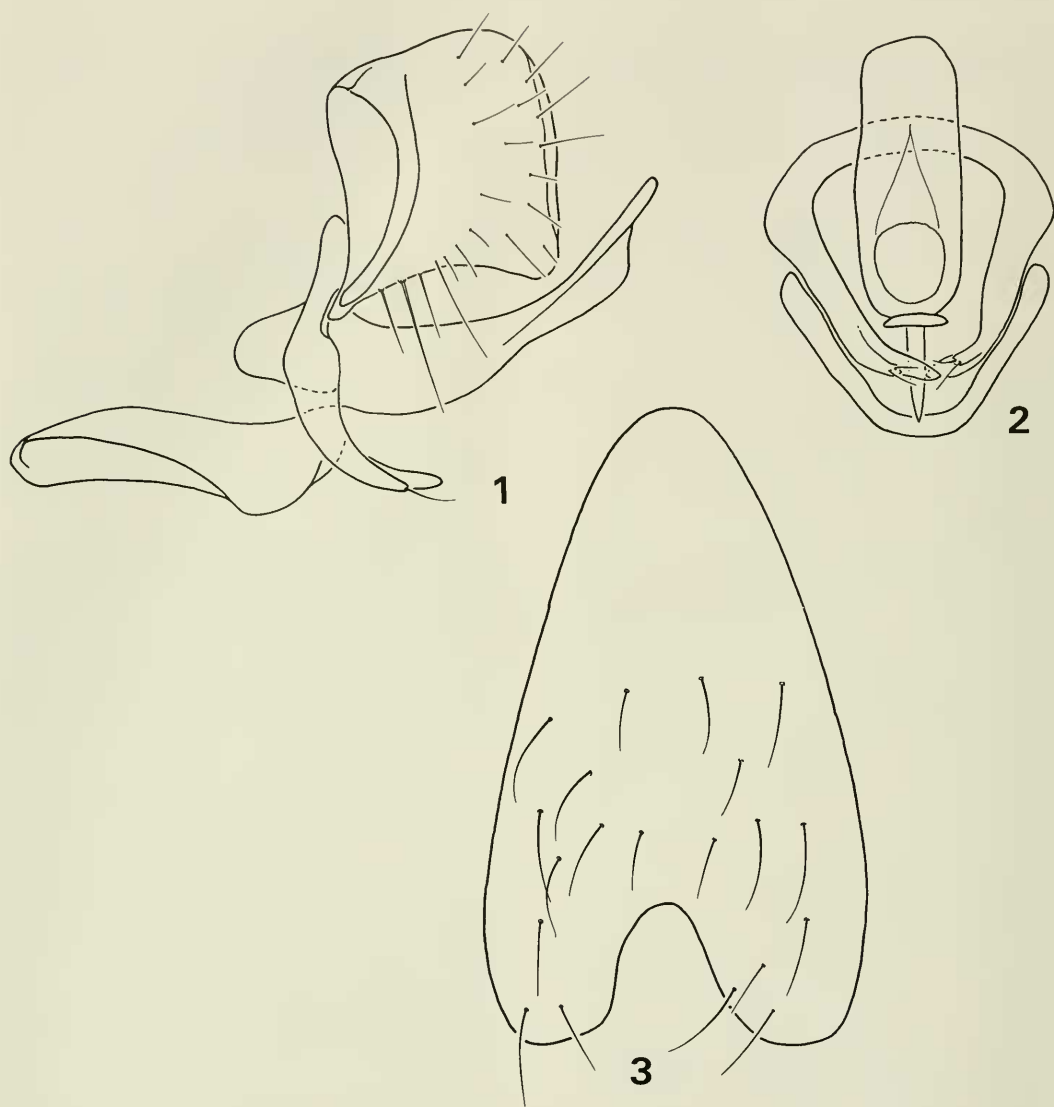
Diagnosis.—This species is distinguished from congeners by the following combina-

tion of characters: Scape, pedicel, and basal half of 1st flagellomere yellow; length of 1st flagellomere twice height; face in profile straight; face mostly uniformly microtomentose and colored, coloration varies depending on angle of view, except for narrow, vertical stripe; length of outer vertical seta less than half inner vertical seta; scutellum densely microtomentose, appearing velvety, dark brown; katepisternum whitish yellow, concolorous with forecoxa; legs entirely yellow, with coxae whitish yellow and apical half of tibiae slightly brownish yellow.

Description.—Minute to small shore flies, length 0.90–1.35 mm.

Head: Frons with distinct, subshiny mesofrons; parafrons densely microtomentose, dark brown, appearing velvety. Fronto-orbital setae very weakly developed and/or lacking, at most with 1–2 hairlike setulae; length of outer vertical seta less than half inner vertical seta, outer seta curved laterally, inner seta very shallowly curved, nearly vertical; ocelli arranged in equilateral triangle, or nearly so. Scape, pedicel, and basal half of 1st flagellomere yellow, apical half of 1st flagellomere brown; length of 1st flagellomere twice height, apex bluntly rounded; arista with 8–9 long, dorsal rays. Face in profile straight at anterior margin; varying in color from different angles, from lateral view mostly yellowish with brownish yellow area at midheight, from anterior view whitish gray, sometimes slightly darker medially at midheight, and with keel-like brown vertical stripe. Eye ratio 0.68–0.71. Gena-to-eye ratio 0.10–0.13. Maxillary palpus yellow; mouthparts mostly yellow to grayish yellow.

Thorax: Mostly dark brown; scutum dark brown with moderately dense whitish gray microtomentum; scutellum with distal 2/3 densely microtomentose, dark brown, appearing velvety, basal 1/3 whitish gray; notopleuron, area of scutum immediately posterior of notopleuron densely microtomentose, dark brown, appearing velvety; anepisternum and anepimeron concolorous, dark



Figs. 1-3. *Lemnaphila longicera*. 1, Male terminalia (epandrium, cercus, surstylus), lateral view. 2, Internal male terminalia (aedeagus, aedeagal apodeme, postgonite, hypandrium, and subepandrial plate), ventral view. 3, Fifth sternite, ventral view.

brown but lighter than notopleuron; katapisternum, meron, and coxae concolorous, whitish yellow. Chaetotaxy: anterior dorso-central seta inserted near level of transverse suture; acrostichal setae lacking; basal scutellar seta about $\frac{1}{3}$ length of apical seta; katapisternal seta lacking. Wing: length 1.08–1.20 mm; width 0.45–0.49 mm; vein R_{4+5} shallowly sinuous, shallowly curved toward posterior margin, than shallowly recurved,

bowed anteriorly; costal vein ratio 1.0–1.07, length of costal section II about equal to section III; M vein ratio 0.42–0.47. Halter knob bright yellow; stem brownish yellow. Legs: femora whitish yellow to yellow basally, becoming more yellow apically; tibiae yellow, becoming slightly darker apically; foretarsi brownish yellow to brown, mid- and hindtarsus slightly lighter than foretarsus, more yellowish.

Abdomen: Dark brown, male 5th tergite subshiny; 5th sternite of male (Fig. 3) well developed, narrowly heart shaped, longer than wide, tapered gradually to narrowly rounded anterior margin, posterior margin deeply emarginate. Male terminalia (Figs. 1–2): Epandrium (Fig. 1) reduced to narrow, fused, lateral phalange at basolateral margin of cercus; cercus (Fig. 1) greatly enlarged, projected posteriorly, bearing 4–5 large setulae at anteroventral margin; subepandrial plate simple, arched, connected ventrally with postgonite; aedeagus in lateral view (Fig. 1) with moderately broad base tapered irregularly thereafter to narrow process, apex narrowly rounded; aedeagal apodeme with ventral keel comparatively long and narrow in lateral view (Fig. 1), slightly asymmetrical; postgonite prominent with rounded apex, bearing setulae about $\frac{3}{4}$ distance from connection with subepandrial plate; hypandrium V-shaped in ventral view (Fig. 2).

Type Material.—The holotype male is labeled “PERU. Loreto: Iquitos [,] 16Feb1984 [,] Wayne N. Mathis/HOLOTYPE *Lemnaphila longicera* ♂ W.N. Mathis & Edmiston USNM [red; species name, gender, and authors handwritten].” The holotype is double mounted (minuten in a block of plastic), is in excellent condition, and is deposited in the USNM. Twenty-two paratypes (8 ♂, 14 ♀; USNM) bear the same label data as the holotype.

Distribution.—*Neotropical*: Peru (Loreto).

Etymology.—The species epithet, *longicera*, alludes to the elongate antenna that, among other characters, distinguishes this species.

Remarks.—Although this species clearly belongs in *Lemnaphila*, it is very distinct structurally (see diagnosis and key) and apparently represents a lineage that has undergone considerable anagenetic evolution. We know nothing about the natural history of the immature stages but suggest that they will be found to be miners in Lemnaceae.

Lemnaphila grossoae Mathis and Edmiston, new species

Diagnosis.—This species is distinguished from congeners by the following combination of characters: Antenna entirely dark brown; length of 1st flagellomere only slightly longer than height; face in lateral view shallowly concave; ventral third of face densely microtomentose, silvery white, distinctly contrasted with blackish brown dorsal portion; mesofrons densely microtomentose, area immediately laterad and anterior of coellar triangle silvery white, otherwise brown to blackish brown; fronto-orbit anterior and posterior of long laterocline fronto-orbital seta silvery white, otherwise velvety blackish brown; scutellum sparsely microtomentose, appearing subshiny to faintly dull, brown; katepisternum brown; femora brown; tibiae and most tarsomeres yellow.

Description.—Small shore flies, length 1.30 mm.

Head: Frons entirely microtomentose, bicolored, brown and silvery white; parafrons and anterior half of fronto-orbit concolorous, densely microtomentose, brownish black, appearing velvety, area immediately laterad and anterior of ocellar triangle silvery white; posterior fronto-orbit (from base of outer vertical seta to base of laterocline fronto-orbital seta) with silvery white microtomentum, concolorous with area laterad and anterior of ocellar triangle. One fronto-orbital seta well developed, length subequal to outer vertical seta, orientation postero-obliquely laterocline to laterocline; other fronto-orbital setae anterior of large seta, at best weakly developed, hairlike; length of outer vertical seta about $\frac{2}{3}$ that of inner vertical seta, outer vertical seta distinctly curved laterally, inner vertical seta very shallowly curved, nearly vertical; ocelli arranged in isosceles triangle, with distance between posterior ocelli greater than between either posterior ocellus and anterior ocellus. Antenna entirely dark brown; length of 1st flagellomere

ere only slightly longer than height; arista with 6–7 long, dorsal rays. Face shallowly concave in lateral view; ventral third of face densely microtomentose, silvery white, distinctly contrasted with blackish brown dorsal portion; dorsal portion of face with very shallow carina, mostly faintly grayish black except for black area on either side of midline just dorsad of silvery white microtomentum. Eye ratio 0.70. Gena-to-eye ratio 0.19. Maxillary palpus blackish brown; mouthparts generally brownish black.

Thorax: Mostly blackish brown; scutum subshiny, sparsely microtomentose; scutellum with moderately dense microtomentum, brownish black, somewhat dull, not velvety appearing like frons except partially along sides; pleuron mostly blackish brown to black except most of anepisternum appearing silvery gray to silvery white. Chaetotaxy: anterior dorsocentral seta inserted behind level of transverse suture; acrostichal setulae sparse anteriorly, in 2 rows, lacking posteriorly; basal scutellar seta about $\frac{1}{3}$ length of apical seta; katapisternal seta well developed, length subequal to posterior anepisternal seta. Wing: length 1.30 mm; width 0.50 mm; vein R_{4+5} shallowly bowed anteriorly; costal vein ratio 1.25; length of costal section II about half of section III; M vein ratio 0.55. Halter knob bright yellow; stem blackish brown. Legs: Femora mostly brown, apices yellowish; tibiae and most tarsomeres yellow, 5th tarsomere brown.

Abdomen: Tergites very sparsely microtomentose to bare, blackish brown.

Type Material.—The holotype female is labeled “ARGENTINA San Miguel de TUCUMAN 2-XII-1976 Col. L. de Grosso [handwritten]/*Lemnaphila lillolana* det. M. Lizarralde de Grosso/PARATIPO [yellow]/COLECCION INST.-FUND M. LILLO (4000)—S.M. TUCUMAN TUCUMAN—ARGENTINA [yellow]/HOLOTYPE *Lemnaphila grossoae* ♀ W.N. Mathis & Edmiston USNM [red; species name, gender, and authors handwritten].” The holotype is double mounted (glued to a large triangle),

is in good condition (glue partially obscuring tarsi), and is deposited in the IML.

Distribution.—*Neotropical*: Argentina (Tucumán).

Etymology.—The species epithet, *grossoae*, is a patronym to honor and recognize the numerous contributions of Dr. Mercedes Lizarralde de Grosso to the study of shore flies, *Lemnaphila* in particular.

Remarks.—This species was misidentified as *L. lillolana* but the pattern of microtomentum and coloration of the head, especially the frons, differs from that species as noted in the diagnosis. In addition to the holotype female, we dissected the male allotype/paratype of *L. lillolana* and discovered that it is likewise not conspecific with *L. lillolana*. Our basis for this conclusion is comparison of the structures of the male terminalia with those that Lizarralde de Grosso (1978:15, figs. 6–13) published. Thus, this male, which lacks its head, may be conspecific with this species.

Lemnaphila lillolana Lizarralde de Grosso

Lemnaphila lillolana Lizarralde de Grosso, 1978:14–17 [immature stages; host plants: *Spirodela biperforata* Kock, *Wolffiella lingulata* (Hegelm.), *Salvinia minima* Baker (Lemnaceae)]; 1989:55 [review, Argentina fauna].-Mathis and Zarnicki, 1995:96 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: Antenna entirely dark brown; length of 1st flagellomere only slightly longer than height; face in lateral view shallowly concave; ventral third of face densely microtomentose, silvery white, distinctly contrasted with blackish brown dorsal portion; mesofrons just anterior of ocellar triangle bare, shiny, blackish brown, contrasted distinctly with densely microtomentose parafrons; posterior fronto-orbit with very small area white; scutellum densely microtomentose, appearing velvety, dark brown; katapisternum brown; femora brown; tibiae and most tarsomeres yellow.

Description.—Small shore flies, length 1.40–1.50 mm.

Head: Frons with mesofrons except for ocellar triangle bare of microtomentum, shiny, blackish brown; parafrons, and anterior half of fronto-orbit concolorous, densely microtomentose, brownish black, appearing velvety; posterior fronto-orbit (from base of outer vertical seta to base of laterocline fronto-orbital seta) with whitish gray microtomentum. One fronto-orbital seta well developed, length subequal to outer vertical seta, orientation postero-obliquely laterocline to laterocline; other fronto-orbital setae anterior of large seta, at best weakly developed, hairlike; length of outer vertical seta about $\frac{2}{3}$ that of inner vertical seta, outer vertical seta distinctly curved laterally, inner vertical seta very shallowly curved, nearly vertical; ocelli arranged in isosceles triangle, with distance between posterior ocelli greater than between either posterior ocellus and anterior ocellus. Antenna entirely dark brown; length of 1st flagellomere only slightly longer than height; arista with 7–8 long, dorsal rays. Face shallowly concave in lateral view; ventral third of face densely microtomentose, silvery white, distinctly contrasted with blackish brown dorsal portion; dorsal portion of face with very shallow carina, mostly faintly grayish black except for black area on either side of midline just dorsad of silvery white microtomentum. Eye ratio 0.75–0.77. Gena-to-eye ratio 0.11–0.12. Maxillary palpus blackish brown; mouthparts generally brownish black.

Thorax: Mostly blackish brown; scutum subshiny, sparsely microtomentose; scutellum with moderately dense microtomentum, brownish black, dull, not velvety appearing like frons; pleuron mostly blackish brown to black except dorsal half of anepisternum from some angles appearing silvery gray. Chaetotaxy: anterior dorsocentral seta inserted behind level of transverse suture; acrostichal setulae sparse anteriorly, in 2 rows, lacking posteriorly; basal scutellar seta about $\frac{1}{3}$ length of apical seta; ka-

tepisternal seta well developed, length subequal to posterior anepisternal seta. Wing: length 1.45–1.60 mm; width 0.60–0.74 mm; vein R_{4+5} shallowly bowed anteriorly; costal vein ratio 1.30–1.33; length of costal section II about half of section III; M vein ratio 0.49–0.50. Halter knob bright yellow; stem blackish brown. Legs: Femora mostly brown, apices yellowish; tibiae and most tarsomeres yellow, 5th tarsomere brown.

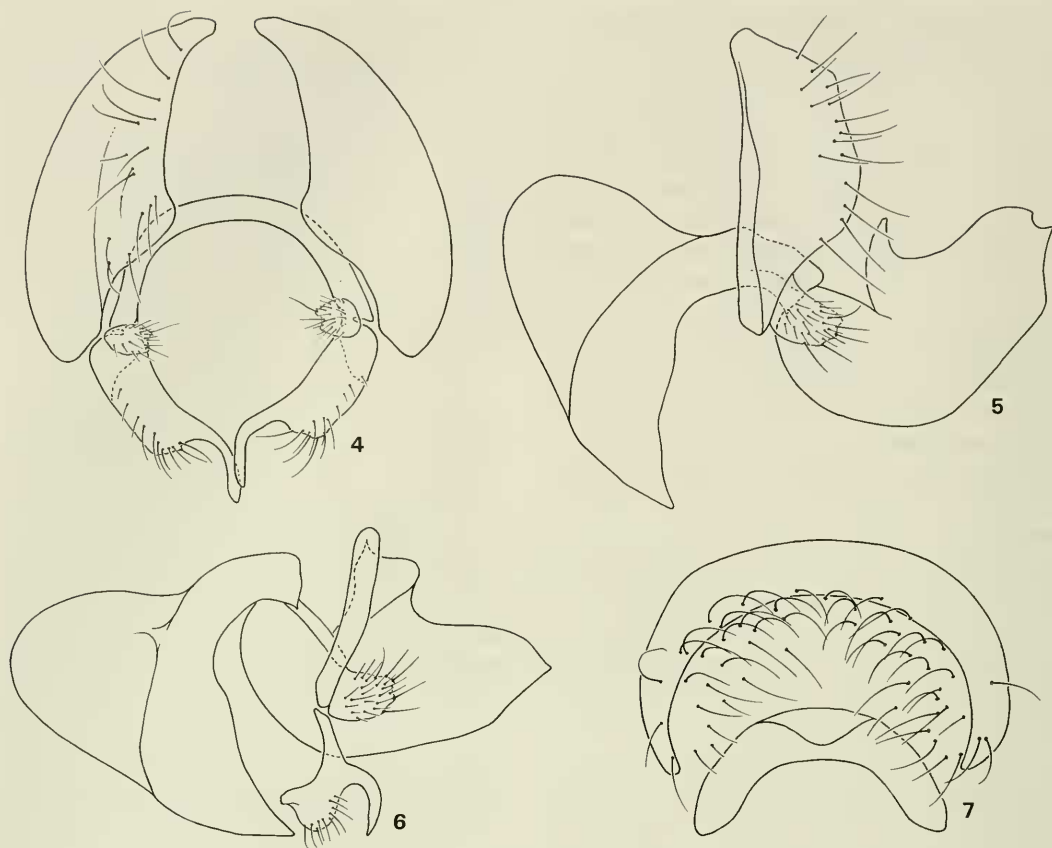
Abdomen: Dark brown.

Type Material.—The holotype female (not a male as indicated in the original description) is labeled “ARGENTINA[.] San Miguel de TUCUMAN[.] 2.XII.1976 [2 Dec 1976] Col. L. de Grosso [handwritten, black margin]/Lemnaphila Lilloana Lizarralde de Grosso det. Lizarralde de Grosso [handwritten, black margin]/HOLOTIPO [red]/COLECCION INST. - FUND. M. LILLO (4000) - S. M. TUCUMAN TUCUMAN - ARGENTINA [yellow].” The holotype is double mounted (glued to moderately large paper triangle), is in fair condition (specimen slightly teneral, eyes and face partially collapsed, right wing with posterior margin folded back on itself), and is deposited in the IML.

Other Specimens Examined.—*ARGENTINA. Tucumán:* San Miguel de Tucumán, 2 Dec 1976, M. Lizarralde de Grosso (6 ♀; paratypes; IML).

Distribution.—*Neotropical:* Argentina (Tucumán).

Remarks.—This species is structurally very similar to *L. neotropica* and is obviously closely related. The only difference that we have discovered in external structures is the shiny mesofrons with the exception of the ocellar triangle (*L. neotropica* has a completely microtomentose, velvety, blackish brown mesofrons). The other differences that Lizarralde de Grosso noted (1978:17) are variable and are within the ranges of either species. No males of this species were available for description and illustration.



Figs. 4–7. *Lemnaphila neotropica*. 4, Male terminalia (epandrium, cercus, surstylus, subepandrial plate, postgonite), posterior view. 5, Same, lateral view. 6, Internal male terminalia, lateral view. 7, Fifth sternite and hypandrium, ventral view.

Lemnaphila neotropica Lizarralde de
Grosso
(Figs. 4–7)

Lemnaphila neotropica Lizarralde de Grosso, 1977:160; 1978:17–18 [biology, immature stages, host plants: *Lemna minima* Philippi, *Hydromystia stolonifera*, parasite: *Hexacola* sp. (Cynipidae)]; 1989:55 [review, Argentina fauna].—Mathis and Zatwarnicki, 1995:96–97 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: Antenna entirely dark brown; length of 1st flagellomere only slightly longer than height; face in lateral view shallowly concave; ventral third of face densely microtomentose, silvery white,

distinctly contrasted with blackish brown dorsal portion; mesofrons and parafrons entirely densely microtomentose, appearing velvety blackish brown; scutellum densely microtomentose, appearing velvety, dark brown; katapisternum brown; femora brown; tibiae and most tarsomeres yellow.

Description.—Minute to small shore flies, length 0.90–1.30 mm.

Head: Frons with mesofrons, parafrons, and anterior half of fronto-orbit concolorous, densely microtomentose, brownish black, appearing velvety; posterior fronto-orbit (from base of outer vertical seta to base of laterocline fronto-orbital seta) with whitish gray microtomentum. One fronto-orbital seta well developed, length subequal to outer vertical seta, orientation

postero-obliquely laterocline to laterocline; other fronto-orbital setae anterior of large seta, at best weakly developed, hair-like; length of outer vertical seta about $\frac{2}{3}$ that of inner vertical seta, outer vertical seta distinctly curved laterally, inner vertical seta very shallowly curved, nearly vertical; ocelli arranged in isosceles triangle, with distance between posterior ocelli greater than between either posterior ocellus and anterior ocellus. Antenna entirely dark brown; length of 1st flagellomere only slightly longer than height; arista with 6–7 long, dorsal rays. Face shallowly concave in lateral view; ventral third of face densely microtomentose, silvery white, distinctly contrasted with blackish brown dorsal portion; dorsal portion of face with very shallow carina, mostly faintly grayish black except for black area on either side of midline just dorsad of silvery white microtomentum. Eye ratio 0.75–0.77. Gena-to-eye ratio 0.11–0.12. Maxillary palpus blackish brown; mouthparts generally brownish black.

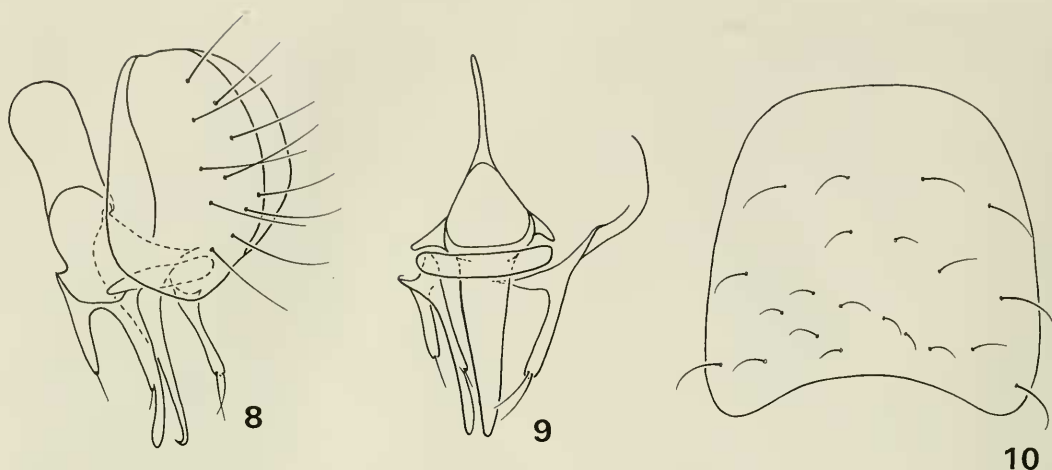
Thorax: Mostly brownish black to black; scutum subshiny, sparsely microtomentose; scutellum with moderately dense microtomentum, brownish black, dull, not velvety appearing like frons; pleuron mostly brownish black to black except dorsal half of anepisternum from some angles appearing silvery gray. Chaetotaxy: anterior dorsocentral seta inserted behind level of transverse suture; acrostichal setulae sparse anteriorly, in 2 rows, lacking posteriorly; basal scutellar seta about $\frac{1}{3}$ length of apical seta; katepisternal seta well developed, length subequal to posterior anepisternal seta. Wing: length 0.80–1.30 mm; width 0.45–0.65 mm; vein R_{4+5} shallowly bowed anteriorly; costal vein ratio 1.60–1.69; length of costal section II slightly less than half of section III; M vein ratio 0.46–0.55. Halter knob bright yellow; stem blackish brown. Legs: Femora mostly brown, apices yellowish; tibiae and most tarsomeres yellow, 5th tarsomere brown.

Abdomen: Dark brown, male 5th tergite

subshiny; 5th sternite of male in ventral view (Fig. 7) much wider than long, broadly and shallowly U-shaped, bearing numerous setulae along posterior margin, these also in membrane between sternite and hypandrium. Male terminalia (Figs. 4–5): Epandrium comparatively well developed as a wide phalange at base of cerci; cerci (Figs. 4–5) well developed, irregularly hemispherical around posteromedial margin, narrowed at dorsal and ventral angles, lateral margin nearly straight in lateral view, shallowly concave in posterior view; surstylus a short process, only slightly longer than wide, bearing numerous setulae, these longer apically; subepandrial plate bandlike in lateral view (Fig. 6), distinctly arched in posterior view (Fig. 4); aedeagus very well developed, angulate in lateral view, robust, especially basiphallus; aedeagal apodeme greatly enlarged, especially expanded keel, keel slightly asymmetrical in lateral view, fanlike; postgonite prominent, heavily sclerotized, base in ventral view rectangular with a narrowed, apical, arched process extended from ventromedial portion of base, apical process parallel sided, apex narrowly rounded; pregonite apparently lacking; hypandrium (Fig. 7) in ventral view a broad, arched band, posterior margin concave, anterior margin convex, with a short, tongue-like, medial process.

Type Material.—The holotype male is labeled “[Argentina. Buenas Aires:] LA PLATA 18/10/71 [18 Oct 1971] COL. [Loiácono-] DIAZ [handwritten; black submargin]/HOLOTIPO [red]/♂/MUSEO DE LA PLATA LEMNAPHILA NEOTROPICA L. DE GROSSO Det LIZARRALDE DE GROSSO [species name and author handwritten; black submargin].” The holotype is double mounted (glued to a large paper triangle), is in fair condition (abdomen missing, some setae misoriented), and is deposited in the UNLP.

Other Specimens Examined.—*ARGENTINA. Buenos Aires:* La Plata, 18 Oct 1971, Loiácono-Díaz (1 ♂, 1 ♀; paratypes; UNLP).



Figs. 8–10. *Lemnaphila scotlandae*. 8, Male terminalia (epandrium, cercus, surstylus, aedeagus, aedeagal apodeme, subepandrial plate, postgonite), lateral view. 9, Internal male terminalia (surstylus shown on right side only, postgonite shown on left side only), dorsal view. 10, Fifth sternite, ventral view.

DOMINICAN REPUBLIC. La Vega: Jarabacoa (1–2 km S; 19°06.9'N, 70°37'W; 520 m), 14–17 May 1998, D. and W. N. Mathis (11 ♂, 4 ♀; USNM).

GRENADA. St. George: Point Salines Airport (W end; 12°00.3'N, 61°47.7'W), 12 Sep 1997, W. N. Mathis (7 ♂, 11 ♀; USNM).

JAMAICA. St. Ann: Runaway Bay (stream bed), Feb 1969, W. W. Wirth (1 ♂; paratype; USNM).

PANAMA. Aguadulce Cocle, 25 Sep 1951, F. S. Blanton (1 ♂; paratype, USNM).

Distribution.—*Neotropical*: Argentina (Buenos Aires, Chaco, Tucumán), Panama, West Indies (Dominican Republic, Grenada, Jamaica).

Remarks.—This species and *L. wirthi* are very similar and obviously closely related. This relationship is established by the following synapomorphies: 1. Aedeagus large, prominent, angulate; 2. 5th sternite of male much wider than long and bearing numerous setulae along posterior, concave margin.

Lemnaphila scotlandae Cresson
(Figs. 8–21)

Lemnaphila scotlandae Cresson, 1933:229
[USA. New York: Tompkins County, Ith-

aca, Fall Creek; HT ♂, ANSP (6501)]; 1944:176 [tribal assignment].—Johannsen, 1935:50–51 [immature stages].—Scotland, 1934:291 [biology, larval miner in *Lemna*]; 1939:713–717 [host plant: *Lemna minor* L. (Lemnaceae); parasitoids: *Opius lemnaphilae* Muesebeck (Braconidae), *Trichopria angustipennis* Muesebeck, *T. paludis* Muesebeck (Diapriidae)]; 1940:322–324 [immature stages, host plants and parasitoids].—Muesebeck, 1939:58–62 [descriptions of parasitoids]; 1979:1146–1147 [catalog of parasitoids, *Trichopria angustipennis* and *T. paludis*].—Wirth, 1965:745 [Nearctic catalog].—Deonier and Regensburg, 1978:155 [records for Ohio].—Marsh, 1979:209 [catalog of parasitoid, *Opius lemnaphilae*].—Ferrar, 1987:169 [summary of biology].—Steinly et al., 1987:166, 168 [records for Illinois, discussion].—Buckingham, 1989:219–221 [parasitoids: *Opius lemnaphilae* Muesebeck (Braconidae), *Trichopria angustipennis* Muesebeck, *T. paludis* Muesebeck (Diapriidae); records for Florida; review of biology].—Mansor and Buckingham, 1989:115–118 [host range].—Foote, 1995:430 [review of biology].—Mathis

and Zatwarnicki, 1995:97 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: Antenna entirely dark brown; length of 1st flagellomere only slightly longer than height; mesofrons subshiny, distinct from densely microtomentose parafrons; face in lateral view shallowly concave; ventral third of face densely microtomentose, appearing velvety, dark brown to golden yellow, depending on angle; scutellum lacking dense microtomentum, gray, not appearing velvety; katapisternum brown; legs brown.

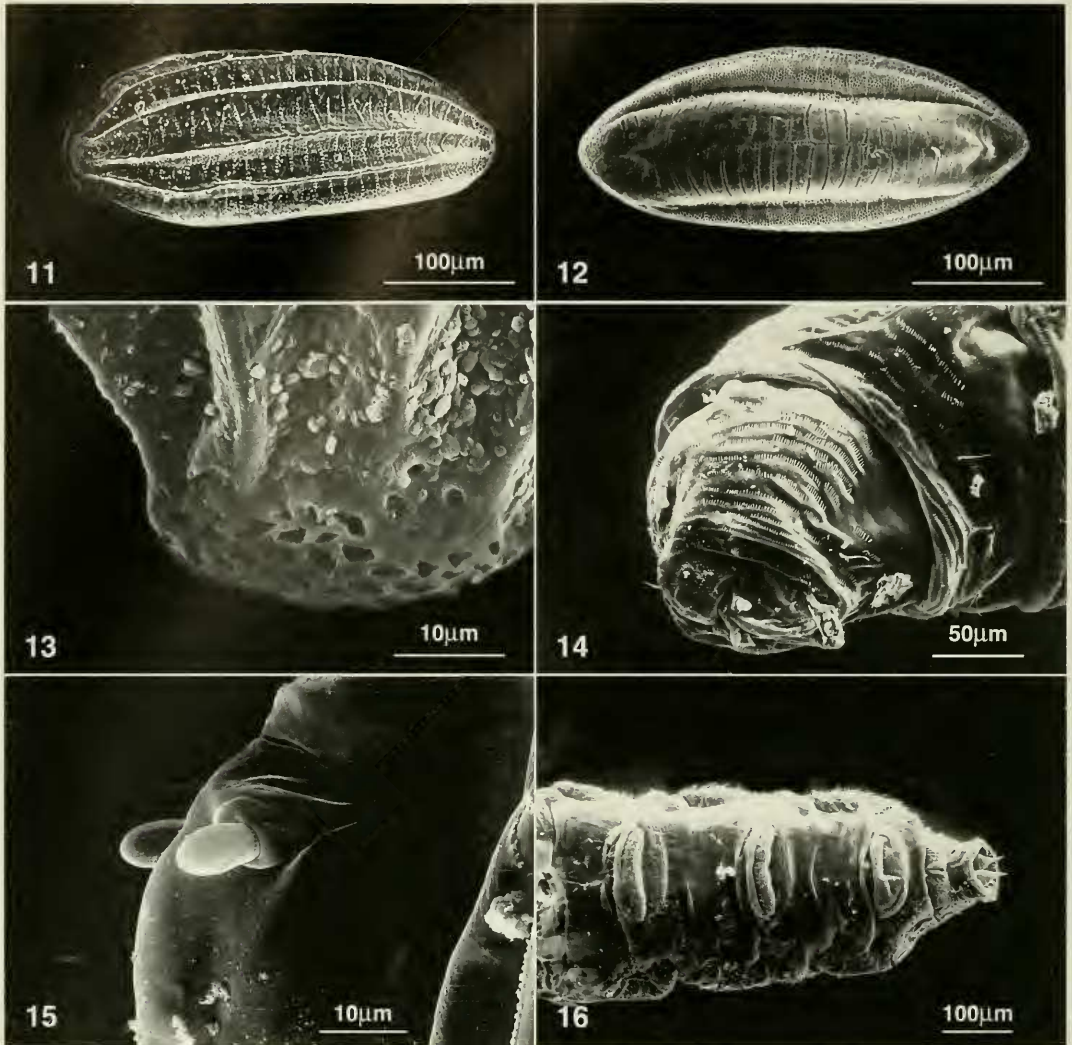
Description.—Minute to very small shore flies, length 0.83–1.2 mm; yellowish brown, dark brown, to black with silvery gray and yellowish silver microtomentum.

Head: Frons generally moderately densely invested with silvery whitish gray microtomentum; mesofrons from ocellar triangle anteriad moderately densely silvery whitish gray microtomentose, subshiny; parafrons brown; fronto-orbit generally concolorous with mesofrons or slightly more brownish. Occiput brown with yellowish silver microtomentum; outer vertical seta lateroocline; length of outer vertical seta about $\frac{3}{4}$ inner vertical seta; inner vertical seta parallel to slightly convergent; fronto-orbital setae minute, hairlike; pseudopostocellar setae prominent, procline and somewhat divergent; paraverticilar setae absent; ocellar setae absent; postocular setae absent; ocelli arranged in isosceles triangle, with distance between posterior ocelli much greater than between either posterior ocellus and anterior ocellus. Antenna entirely dark brown; length of 1st flagellomere only slightly longer than its height; arista bearing 5–7 rays along dorsum. Facial background coloration shiny dark brown with sparse silvery gray microtomentum. Oral margin slightly protruded dorsally. Face with transverse crease at about ventral third, shallowly concave in lateral view, ventral third slightly angled forward, densely microtomentose,

dark brown. Parafacial band shiny dark brown. Eye ratio 0.78–0.83. Gena-to-eye ratio 0.14–0.17. Gena and postgena brown with sparse silvery yellow microtomentum; parafacial setae minute; gena bearing small black setulae. Maxillary palpus dark brown with prominent setae; prementum shiny dark brown, bulbous.

Thorax: Mesonotum brown with silvery yellow microtomentum; scutellum lacking microtomentum or microtomentum sparse, not appearing velvety; scutum length 0.29–0.43 mm; scutellar length 0.10–0.17 mm; subscutellum brown with yellowish silver microtomentum; anepisternum with dorsal half brown with dense silvery gray microtomentum, ventral half with sparse silvery and golden microtomentum; katapisternum brown with sparse silvery golden microtomentum; anatergite brown with yellowish silver microtomentum. Chaetotaxy: anterior dorsocentral seta inserted near level of transverse suture; acrostichal setulae lacking; scutellar setae with anterolateral setae $\frac{3}{4}$ length of posteromedial setae and mediolateral setulae; katapisternal seta weakly developed, hairlike, much shorter than posterior anepisternal seta. Wing: length 1.02–1.44 mm; width 0.42–0.61 mm; vein R_{4+5} shallowly bowed anteriorly; costal vein ratio 1.76–1.85, with length of costal section II about half costal section III; M vein ratio 0.46–0.55. Halter knob bright yellow; stem blackish brown. Legs: yellowish brown to brown; tarsomeres 1–4 yellowish brown, darker distally; tarsomere 5 brown.

Abdomen: Tergite 3 length, males 0.13–0.17 mm, females 0.14–0.20 mm; tergite 4 length, males 0.18–0.20 mm, females 0.18–0.20 mm. Background coloration brown to dark brown. Tergites 1–5 covered with sparse yellow microtomentum; 5th sternite slightly longer than wide, tapered slightly anteriorly, bearing numerous setulae. Male Terminalia (Figs. 8–9): Epandrium much reduced, as a small, lateral phalange at base of fused cercus; cercus comparatively greatly enlarged, height nearly equal to width of 5th sternite of male; subepandrial plate an



Figs. 11–16. Scanning electron micrographs of *Lemnaphila scotlandae*. 11, Egg, dorsal view. 12, Same, ventral view. 13, Micropylar end of egg, ventral view. 14, Third-instar larva, cephalic end, lateroblique view. 15, Same, antennae. 16, Same, posterior end, ventral view.

arched, narrow, bandlike plate; surstylus (Fig. 8) a long, narrow, parallel-sided process bearing 2 apical setulae; aedeagus cornucopialike in lateral view (Fig. 8), with broad base, tapered to narrow apex that is hooked; aedeagal apodeme with keel comparatively long and narrow in lateral view, essentially symmetrical; subepandrial plate forming rounded arch, connected ventrally with postgonite; postgonite (Fig. 8) prominent with a posterior and anterior process; posterior gonapophysis prominent with api-

cal $\frac{1}{3}$ parallel-sided, apex rounded, ventrally projected setula about $\frac{2}{3}$ distance from connection with subepandrial plate; anterior gonapophysis in lateral view (Fig. 8) a small, narrow, tapered process about $\frac{1}{2}$ length of surstylus, bearing apical setulae; hypandrium (Fig. 10) narrowly V-shaped.

Type Material.—The holotype male is labeled “♂/Fall Creek, Ithaca, N[ew]. Y[ork]./M. B. Scotland VII 25–46 [sic; Jul 25–26], 1933/TYPE No. 6501 *Lemnaphila SCOTLANDAE* E.T. Cresson, Jr. [red;

number and species name handwritten].” The holotype is double mounted (glued to a pin in a rectangular block of cork), is in excellent condition (slightly teneral), and is deposited in the ANSP (6501).

Other Specimens Examined.—NEARCTIC. CANADA. ONTARIO. Guelph, 12 Jan 1976, J. M. Cumming (14 ♂, 16 ♀; GUE); 16 Jan 1976, J. M. Cumming (5 ♀; GUE); 8 Aug 1978, W. A. Attwater (3 ♂, 5 ♀; GUE); Limehouse, 1 Sep 1974, R. E. Roughley (1 ♂, 1 ♀; GUE); 2 Sep 1974, R. E. Roughley (1 ♂, 5 ♀; CNC, GUE); 6 Oct 1974, R. E. Roughley (on *Lemna minor* in Black Creek), (1 ♀; GUE); Ottawa, 196?, J. G. Chillcott (2 ♂, 2 ♀; CNC); Wainfleet Bog (8 km S Welland), 14–28 Sep 1987, A. Stirling (2 ♂; WSU).

UNITED STATES. FLORIDA. Alachua: Gainesville, 13–31 Oct 1986 (*Lemna valdiviana*: pools at Division of Plant Industry), G. R. Buckingham (4 ♂, 14 ♀, 1?; JEPC); Pierce’s Homestead (Malaise trap; S9-T10S-R18E), 11 May 1974, W. H. Pierce (1 ♀; USNM). Broward: Ft. Lauderdale (*Lemna valdiviana*), 14 Nov 1988, G. R. Buckingham (1 ♂; USNM). Putnam: Rodman Reservoir (*Lemna minor*), 6 Oct 1987, G. R. Buckingham (1 ♂, 1 ♀; USNM). Sumter: Lake Okahumpka (*Lemna valdiviana*), 22 Oct 1987, G. R. Buckingham (1 ♀; USNM). MICHIGAN. Clinton: Bath, 10 Oct 1965, (1 ♀; USNM). NEW YORK. Tompkins: Ithaca, Fall Creek, 25–26 Jul 1933, M. B. Scotland (12 ♂, 11 ♀; allotype; AMNH, ANSP, BMNH, CU, USNM); Ithaca, Sep 1933, M. B. Scotland (7 ♂, 11 ♀; CU, USNM). OHIO. Portage: Kent (near Kent State University stadium), 23 May–4 Aug 1986, 1987, J. Edmiston (12 ♂, 12 ♀; JEPC); Kent, 24 Jun–2 Sep 1987 (lab reared), J. Edmiston (9 ♂, 14 ♀; JEPC). Franklin: Columbus (Mirror Lake), 23 Aug 1919, W. C. Kraatz (1 ♂; OHSU). Geauga: LaDue Reservoir (41°22.2’N, 80°13.4’W; duckweed), 12 Sep 1976, B. A. Steinly (32 ♂, 21 ♀; USNM).

Distribution.—Nearctic: Canada (ON), USA (FL, IL, MI, NY, OH).

Natural History.—Adult *L. scotlandae* are commonly found on or flying over the surface of floating duckweed thalli. The adults utilize the *Lemna* for food, leaving characteristic elongate gouges on the surface of the thallus. Seasonal distribution and overwintering stages are unknown; adults, however, have been collected in late November, suggesting that adults are able to survive the cold season like other north-temperate Ephydriidae. Adults collected from the field and reared in the laboratory lived between 2–21 days ($n = 13$).

Females lay eggs on the margin of a *Lemna* thallus, usually one egg per thallus. Females collected from the field and reared in the laboratory laid up to 41 eggs per day, averaging 21–26 eggs per day ($n = 11$) during their first four days in the laboratory. One female laid 334 eggs during 20 days.

Eggs hatch in 4–6 days ($x = 4.21$; $n = 10$), after which the first-instar larvae begin feeding on thallus tissue. Burrowing through the duckweed, the first-instar larvae feed for 1–3 days ($x = 1.92$; $n = 10$) before molting; second-instar larvae feed for 1–4 days ($x = 2.62$; $n = 10$) before molting; third-instar larvae feed for 2–7 days ($x = 4.85$; $n = 10$) before pupariation occurs within the hollowed-out duckweed thallus. The pupal period ranged between 6–8 days ($x = 7.15$ days; $n = 10$).

Although the immatures and adults of this species are very tiny, three hymenopterous parasitoids, as noted in the synonymy, have been reared from puparia (Muesebeck 1939, Scotland 1939, Buckingham 1987).

DESCRIPTION OF IMMATURE STAGES

Egg (Figs. 11–12).—Length 0.35–0.37 mm ($x = 0.36$; $n = 12$); width 0.13–0.17 ($x = 0.16$; $n = 12$); ovoid, ends bluntly rounded; micropylar end porous; 4 longitudinal ridges dorsally with parallel rows of minute pores between ridges; flattened ventrally with medioventral rows of minute pores and laterally with parallel rows of minute pores. Chorion light brown.

Mature third-instar larva (Figs. 20–21).—Length 1.11–1.34 ($x = 1.24$; $n = 5$); width 0.22–0.32 ($x = 0.28$; $n = 5$). vermiform, 12 segmented, white. Anterior end blunt with ventrally projected mandibles, posterior end with medioventrally projected spiracles. Integument covered with minute setulae. *Cephalic segment* (segment 1, pseudocephalic segment): antenna 2 segmented with rounded socket, proximal antennal segment minute, circular; distal antennal segment ovoid, greater than $10\times$ length of proximal segment, lateroventrally with rounded sensory pits.

Segment 2 (prothoracic segment): ventrally and laterally with rows of comblike setae, projected dorsomedially over cephalic segment. Segment 3: longest segment, $1\frac{1}{3}$ length of segment 2 with rows of comblike setae. Segments 3–11 similar, rounded, ventral surface with creeping welts; welts of segments 3 and 4 small; welts of segments 5–11 large. Segment 12 with perianal pad ventrally and posterior spiracles ventromedially; perianal pad bilobed, each lobe ovoid; posterior spiracle with cylindrical base and conical projection; conical projection approximately twice as long as cylindrical base and tapered to point.

Cephalopharyngeal skeleton (Figs. 17–19): A-PDC 0.20–0.21 mm ($n = 7$), A-VDC 0.18–0.20 mm ($n = 7$), PDC-VDC 0.08 mm ($n = 7$). Mandibles fused dorsally, anteriorly pointed, posteriorly broadened. Hypopharyngeal sclerite minute, posteriorly rounded, anteriorly slightly indented. Tentoropharyngeal sclerite anteriorly roundly pointed with anteroventral projection, dorsal cornu posteriorly sharply pointed, ventral cornu posteriorly broadened. First- and second-instar larvae similar. Distinguishable by size of tentoropharyngeal sclerite.

Puparium (Fig. 21).—Length 1.17–1.36 ($x = 1.28$; $n = 13$); width 0.53–0.60 ($x = 0.56$; $n = 13$); width broadest posteromedially in ventral view, tapering at each end; anterior end slightly curved ventrally, broadly rounded with remnants of cephal-

opharyngeal skeleton clearly visible; posterior end slightly curved ventrally, spiracle remnants dark, perianal pad remnants visible; margins of puparium smooth. Color uniformly pale brown except for black cephalopharyngeal skeleton remnants.

Remarks.—This species is commonly called the *Lemna* fly (Scotland 1934, 1939, 1940) or the duckweed miner, and the adults and immature stages live entirely in and around duckweed (Lemnaceae). Miss Minnie B. Scotland (1933), after whom the species was named, first reared *L. scotlandae* from duckweed (*Lemna minor* L.) that was collected in a fish hatchery at Fall Creek near Ithaca, New York. The species is now known to occur from southern Canada to northern Florida and west to Illinois.

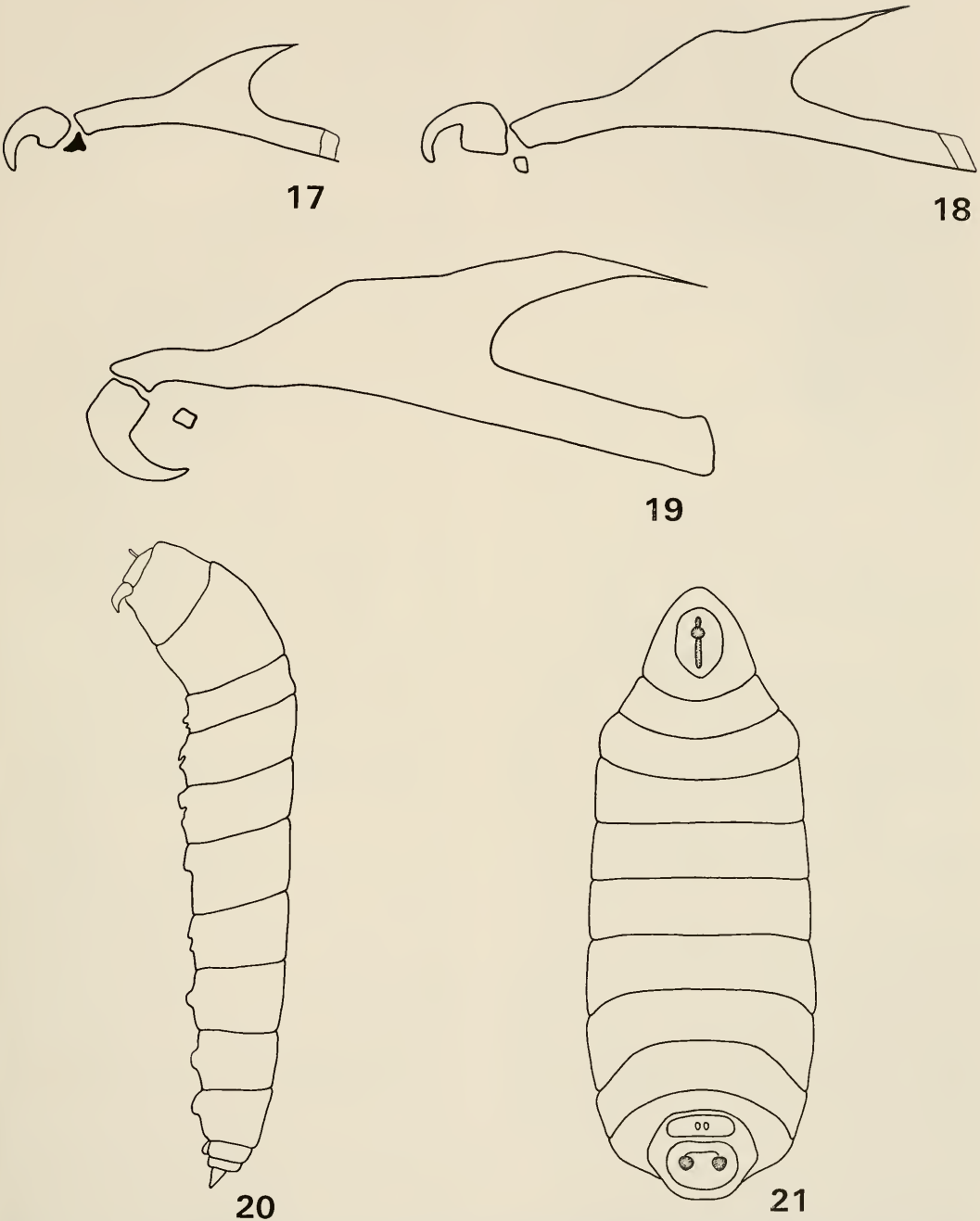
Lemnaphila wirthi Lizarralde de Grosso
(Figs. 22–26)

Lemnaphila wirthi Lizarralde de Grosso, 1977:163; 1978:18–19 [review, description of male terminalia]; 1989:55 [review, Argentina fauna].—Mathis and Zawnicki, 1995:97 [world catalog].

Diagnosis.—This species is distinguished from congeners by the following combination of characters: Antenna entirely dark brown; length of 1st flagellomere only slightly longer than height; face in lateral view shallowly concave; ventral third of face densely microtomentose, blackish brown, concolorous with dorsal portion of face; scutellum densely microtomentose, appearing velvety, dark brown; katapisternum brown; coxae, femora, and tibiae yellow.

Description.—Minute to very small shore flies, length 0.95–1.20 mm.

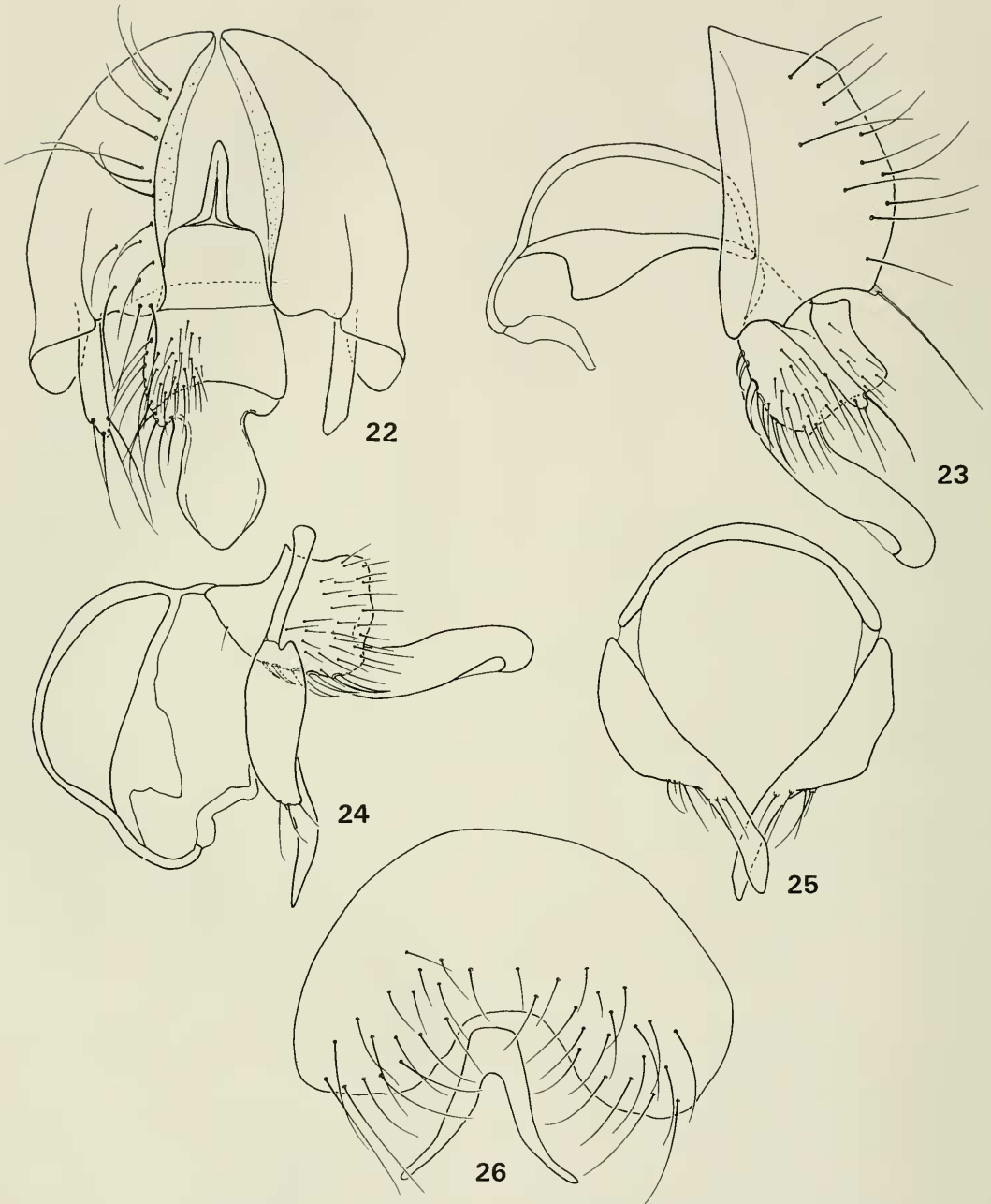
Head: Frons with mesofrons, parafrons, and anterior half of fronto-orbit concolorous, densely microtomentose, brownish black, appearing velvety; posterior fronto-orbit (from base of outer vertical seta to base of lateroocline fronto-orbital seta) with whitish gray microtomentum. One fronto-orbital seta well developed, length



Figs. 17–21. *Lemnaphila scotlandae*. 17, Cephalopharyngeal skeleton, first-instar larva. 18, Same, second-instar larva. 19, Same, third-instar larva. 20, Third-instar larva, lateral view. 21, Puparium, ventral view.

subequal to outer vertical seta, orientation postero-obliquely laterocline to laterocline; other fronto-orbital setae anterior of large seta, at best weakly developed, hair-

like; length of outer vertical seta about $\frac{2}{3}$ that of inner vertical seta, outer vertical seta distinctly curved laterally, inner vertical seta very shallowly curved, nearly vertical;



Figs. 22-26. *Lemnaphila wirthi*. 22, Male terminalia (epandrium, cercus, surstylus, aedeagus, aedeagal apodeme), posterior view. 23, Same (with addition of postgonite), lateral view. 24, Internal male terminalia, lateral view. 25, Postgonite and subepandrial plate, ventral lateral view. 26, Fifth sternite and hypandrium, ventral view.

ocelli arranged in isosceles triangle, with distance between posterior ocelli greater than between either posterior ocellus and anterior ocellus. Antenna entirely dark

brown; length of 1st flagellomere only slightly longer than height; arista with 6-7 long, dorsal rays. Face with shallowly concave in lateral view; ventral third of face

densely microtomentose, concolorous with frons; dorsal portion of face with very shallow carina, mostly black except shiny black carina. Eye ratio 0.68–0.74. Gena-to-eye ratio 0.09–0.11. Maxillary palpus blackish brown; mouthparts generally brownish black.

Thorax: Mostly brownish black to black; scutum subshiny, sparsely microtomentose; scutellum with dense microtomentum, brownish black, not shiny, but velvety appearing like frons; pleuron mostly brownish black to black except dorsal half of anepisternum from some angles appearing silvery gray. Chaetotaxy: anterior dorsocentral seta inserted behind level of transverse suture; acrostichal setulae sparse anteriorly, in 2 rows, lacking posteriorly; basal scutellar seta about $\frac{1}{3}$ length of apical seta; katepisternal seta well developed, length subequal to posterior anepisternal seta. Wing: length 1.08–1.24 mm; width 0.45–0.57 mm; vein R_{4+5} mostly straight to very shallowly bowed anteriorly; costal vein ratio 1.5–1.73; length of costal section II about half of section III; M vein ratio 0.44–0.49. Halter knob bright yellow; stem brownish yellow. Legs: yellow except for brown 5th tarsomeres.

Abdomen: Dark brown, male 5th tergite subshiny; 5th sternite of male (Fig. 26) broadly and shallowly U-shaped, thickly formed, bearing numerous setulae along posterior margin and on membrane immediately adjacent. Male terminalia (Figs. 22–24): Epandrium (Figs. 22–23) comparatively well developed as a phalange at ventrobasal angle of cercus; cerci very well developed, in lateral view (Fig. 23) irregularly hemispherical around posteromedial margin, basolateral margin even, nearly straight in lateral view, shallowly concave in posterior view; surstylus (Figs. 22–23) long, slender, mostly parallel sided, apical $\frac{2}{3}$ well sclerotized, bearing several setulae along length, apex rounded; subepandrial plate (Figs. 24–25) evenly arched, slender, band-like in lateral view (Fig. 24); aedeagus angulate in lateral view (Fig. 24), basiphallus

in lateral view somewhat quadrate with distiphallus extended from ventral portion of basiphallus, distiphallus long, slender, shallowly sinuous, apex recurved; aedeagal apodeme (Fig. 24) enlarged, in lateral view semioval with keel prominent, wide; postgonite in lateral view long and conspicuously sinuous, base moderately slender, apical $\frac{1}{3}$ more slender, apex acutely pointed, apices cruciate in ventral view (Fig. 25); hypandrium in ventral view (Fig. 26) narrowly V-shaped with arms slightly flared apically, base wide and bluntly rounded.

Type Material.—The holotype female is labeled “ECUADOR. Manabi[:] Estero Balsa 9 Sept 1955/Collr. Levi-Castillo/Lemnaphila 2 n sp. det WWirth '60 [?]/LEMNAPHILA WIRTH L. DE GROSSO [handwritten]./HOLOTYPE [red].” The holotype is double mounted (glued to a paper triangle), is in good condition (right wing in glue, some setae broken), and is deposited in the USNM.

Other Specimens Examined.—NEOTROPICAL. *DOMINICAN REPUBLIC*. *La Vega*: Jarabacoa (1–2 km S; 19°06.9'N, 70°37'W; 520 m), 8–21 May 1995, 1998, W. N. Mathis (29♂, 13♀; USNM).

Distribution.—*Neotropical*: Argentina (Tucumán), Ecuador, West Indies (Dominican Republic).

Remarks.—The specimens from the Dominican Republic are a major extension in the known range of this species, and emphasizes the apparent lack of collecting this species and *Lemnaphila* generally. We now know this species from Argentina in the south to Ecuador and the Dominican Republic in the north.

PHYLOGENETIC CONSIDERATIONS

Lemnaphila, as discussed previously (generic diagnosis and discussion), is similar and related to *Hydrellia* and *Cavatorella*, and these three genera comprise the tribe Hydrelliini in the subfamily Hydrelliinae. The tribe Hydrelliini is distinguished from other tribes of Hydrelliinae by the following characters: specimens usually dull and

densely microtomentose (some species secondarily sparsely microtomentose, subshiny, blackish); ocellar setae seldom as strong as pseudopostocellar setae, usually much weaker; eye bearing numerous short, interfacetal, fluted setulae; postsutural supra-alar seta usually short, not longer than posterior notopleural seta; posterior notopleural seta at same level as anterior seta (independently and secondarily inserted above level of anterior seta in *Lemnaphila*, as in *Atissini*); costa extended to vein M; midtibiae lacking dorsal, spinelike setae.

Within Hydrelliini, the three included genera are distinguished from each other by the characters noted in the generic key (p. 654). The relationships among these genera, however, are unresolved and remain problematic. For example, although *Lemnaphila* and its included species are a well-corroborated, monophyletic lineage (see below), this lineage may eventually be found to be an included lineage within *Hydrellia*, i.e., *Hydrellia* lacks characterization by synapomorphies and its monophyly is unsubstantiated. *Cavatorella* may likewise be an included lineage within *Hydrellia*, perhaps closely related to *Lemnaphila*.

Synapomorphies that conclusively establish the monophyly of *Lemnaphila* are: 1. Ocellar setae lacking (also lacking in some species of *Hydrellia*); 2. Prescutellar acrostichal seta lacking; 3. Vein R_{2+3} short with costal section II shorter than section III (a shortened R_{2+3} also occurs in some species of *Hydrellia* and in *Cavatorella*); 4. Posterior notopleural seta inserted near dorsal (sutural) angle, clearly higher than the level of the anterior seta; 5. Anepisternum bearing a single seta along the posterior margin; 6. Epandrium weakly developed, incomplete dorsally, with membranous gap between lateral extensions, these extensions are as narrow, lateral phalanges at base of cerci; 7. Cerci fused with medial margin of epandrium; 8. Surstylus reduced to a simple, small process at the ventral margin of the fused epandrium/cerci complex; 9. Larvae mining the thalli of Lemnaceae (*Hydrellia*

albilabris (Meigen) from the Old World also mines the thalli of *Lemna* (Mathis and Zatzwornicki 1995)). The mining habit of *H. albilabris* in *Lemna* apparently arose independently. We have examined specimens of *H. albilabris* to verify that they are not closely related to *Lemnaphila*.

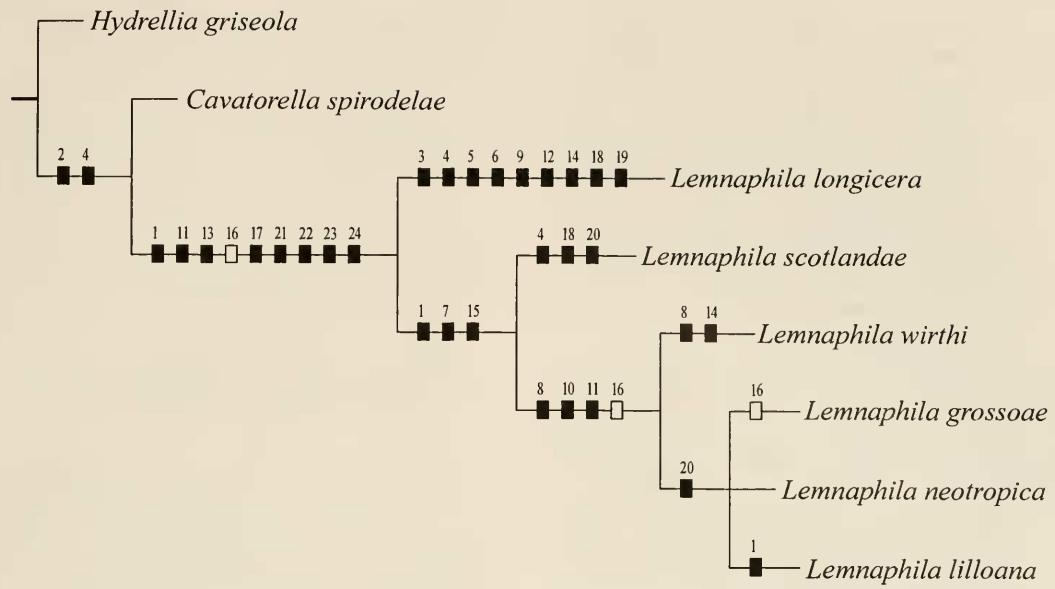
In the presentation on species-level relationships that follows, the characters used in the analysis are noted first. Each character is immediately followed by a discussion to explain its states and to provide perspective and any qualifying comments about that character. After presentation of the information on character evidence, an hypothesis of the cladistic relationships is presented and briefly discussed. The cladogram (Fig. 27) is the primary mode to convey relationships, and the discussion is to supplement the cladogram and is intended only to complement the latter. In the discussion of character data, a "0" indicates the state of the outgroup; a "1" or "2" indicate the respectively more derived states. All multistate characters (1, 4, 8, 11, 14, 18, 20) were treated as nonadditive characters (-), and characters 5, 6, and 9, which are autapomorphies for *L. longicera*, were made inactive (I) for the analysis, such as calculation of the consistency index. The numbers used in the presentation are the same as those on the cladogram (Fig. 27), and the sequence is the same as noted in the character matrix (Table 1).

The other two genera of Hydrelliini, *Hydrellia* and *Cavatorella*, were selected as outgroups. As the exemplar of *Hydrellia*, we chose the widespread type species of the genus, *H. griseola* (Fallén), and for *Cavatorella*, which is monotypic, we studied *C. spirodelae* Deonier, which occurs in China and Japan (Deonier 1995). *Hydrellia* is represented by over 200 species worldwide (Mathis and Zatzwornicki 1995).

CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

Head:

1. *Vestiture of mesofrons*: moderately mi-



Figs. 27. Cladogram depicting hypothetical cladistic relationships among species of *Lemnaphila*.

crotomentose, appearing mostly dull (0); sparsely microtomentose, subshiny (1); densely microtomentose, appearing velvety black or whitish (2); mesofrons, except ocellar triangle, bare, shiny (3). This multistate character is treated as nonadditive.

- 2. *Ocellar setae*: present (laterad of anterior ocellus, smaller than pseudopostocellar setae) (0); lacking or greatly reduced (1).
- 3. *Arrangement of ocelli*: ocelli forming an isosceles triangle with distance be-

tween posterior ocelli about twice that between either posterior ocellus and anterior ocellus (0); ocelli forming an equilateral triangle or with distance between posterior ocelli only slightly more than between either posterior ocellus and anterior ocellus (1).

- 4. *Fronto-orbital setae*: anterior fronto-orbital seta proclinate, smaller than posterior seta, which is laterobliquely reclinate (0); posterior seta elongate, oriented laterally (1); both setae reduced but evident (2); both setae greatly reduced or lacking (3). This multistate character is treated as nonadditive.
- 5. *Color of antenna*: generally unicolorous, most brownish black but sometimes yellowish (0); scape, pedicel, and basal half of 1st flagellomere yellow (1). The derived state of this character is an autapomorphy for *L. longicera* and is therefore treated as an inactive character in the analysis.
- 6. *Length of 1st flagellomere*: about equal to or slightly greater than height (0); twice height (1). The derived state of this character is an autapomorphy for

Table 1. Matrix of characters and taxa used in the cladistic analysis of *Lemnaphila* (numbers for characters correspond with those used in the text).

	000000000	11111111112	222	2
	123456789	01234567890	123	4
Hydrellia	000000000	00000000000	000	0
Cavatorella	000100000	10000000000	000	0
<i>L. longicera</i>	111311001	02112011210	111	?
<i>L. grossoae</i>	210100110	11010121001	111	1
<i>L. scotlandae</i>	210200100	02010111102	111	1
<i>L. wirthi</i>	210100120	11011101000	111	1
<i>L. neotropica</i>	210100110	11010101001	111	1
<i>L. lilloana</i>	310100110	11010101001	111	1

L. longicera and is therefore treated as an inactive character in the analysis.

7. *Shape of face in lateral view*: face straight (0); shallowly concave, usually with a shallow, transverse groove (1).
8. *Facial vestiture*: face mostly uniformly microtomentose, color varying, depending on angle of view, except for narrow, vertical stripe (0); ventral third of face densely microtomentose, silvery white, distinctly contrasted with blackish brown dorsal portion (1); ventral third of face densely microtomentose, dark brown (2). This multistate character is treated as nonadditive.
9. *Length of outer vertical seta*: about $\frac{2}{3}$ – $\frac{3}{4}$ length of inner vertical seta (0); less than half inner vertical seta (1). The derived state of this character is an autapomorphy for *L. longicera* and is therefore treated as an inactive character in the analysis.

Thorax:

10. *Position of anterior dorsocentral seta*: inserted posterior of transverse suture (0); inserted at level of transverse suture (1).
11. *Acrostichal setulae*: numerous setulae and 1 well-developed pair of prescutellar setae (0); sparse setulae anteriorly, in 2 rows, lacking posteriorly, including prescutellar pair (1); lacking (2). This multistate character is treated as nonadditive.
12. *Comparative length of basal scutellar seta*: long, from $\frac{1}{2}$ to being subequal to length of apical seta (0); short, about $\frac{1}{3}$ length of apical seta (1).
13. *Position of posterior notopleural seta*: inserted at about same level as anterior seta (0); inserted at elevated position relative to anterior seta (1).
14. *Scutellar vestiture*: moderately densely microtomentose, not appearing velvety (0); scutellum densely microtomentose, somewhat appearing velvety (1); scutellum densely microtomentose, appearing velvety, dark brown, similar to notopleural patch (2). This multistate character is treated as nonadditive.
15. *Length of costal sections II and III*: costal sections II and III about equal in length, vein R_{2+3} relatively long (0); costal section III considerably longer than II, vein R_{2+3} relatively short (1).
16. *Shape of anal angle of wing*: deeply rounded, greatest depth equal to or greater than distance between apices of vein R_{4+5} and M (0); very shallow rounded, greatest depth conspicuously less than distance between apices of vein R_{4+5} and M (1).
17. *Number of setae and setulae along posterior margin of anepisternum*: 1 large seta and 1–2 setulae (0); 1 seta, setulae greatly reduced or lacking (1).
18. *Presence or absence of katepisternal seta*: seta well developed, length subequal to posterior anepisternal seta (0); seta greatly reduced (1); or lacking (2). This multistate character is treated as nonadditive.
19. *Color of katepisternum*: brown (0); whitish yellow, concolorous with fore-coxa (1).
20. *Color of legs*: legs entirely yellowish, with coxae whitish yellow and apical half of tibiae slightly brownish yellow (0); femora brown, tibiae and most tarsomeres yellow (1); legs unicolorous, brown (2). This multistate character is treated as nonadditive.

Abdomen:

21. *Development of epandrium at dorsum*: dorsum of epandrium well developed to weakly developed (0); epandrium incomplete dorsally with membranous gap between lateral phalanges (1).
22. *Condition of cercus relative to epandrium*: cerci free from epandrium (0); cerci fused laterally to medial margin of epandrial phalange (1).
23. *Development of surstyli*: generally well developed structures at ventral margin of epandrium (0); reduced to simple

Table 2. Analysis of characters based on the cladogram (Fig. 27).

Character	1	2	3	4	5	6	7	8	9	10	11	12
Steps	3	1	1	3	1	1	1	2	1	1	2	1
Con. Index	100	100	100	100	100	100	100	100	100	100	100	100
Ret. Index	100	100	100	100	100	100	100	100	100	100	100	100
Character	13	14	15	16	17	18	19	20	21	22	23	24
Steps	1	2	1	4	1	2	1	2	1	1	1	1
Con. Index	100	100	100	50	100	100	100	100	100	100	100	100
Ret. Index	100	100	100	0	100	100	100	100	100	100	100	100

small process at ventral margin of the fused epandrial/cercal complex (1).

Behavior:

24. *Feeding preference*: miner in various, mostly aquatic plants (0); miner in the thalli of Lemnaceae (1). Lacking rearing records for *L. lonicera*, we coded this character as a ? for this species. Like all other members of *Lemnaphila*, however, we anticipate and predict that this species will also be found to be a miner in aquatic plants of Lemnaceae.

ANALYSIS

Using the implicit enumeration (ie*) option of Hennig86, four most and equally parsimonious trees were generated, each with a length of 34 steps and consistency and retention indices of 0.91 and 0.86 respectively. The basal nodes in each of these cladograms are identical, with variation only in the more derived four species (the apical 2–3 nodes).

The matrix was then subjected iteratively to successive weighing (xs w, ie*, cc) to determine a character's contribution or weight and to find cladograms supported by the most consistent characters (Carpenter 1988, Dietrich and McKamey 1995). Suc-

cessive weighing produced a single cladogram (Fig. 27) that is identical to one of the first four and is our cladogram of choice. The analysis of the characters for this cladogram is given in Table 2 and the weights of the various characters is given in Table 3.

Hydrellia was consistently the basal outgroup, with *Cavatorella* as the more immediate outgroup to *Lemnaphila*. Although the placement of *Cavatorella* as the sister group to *Lemnaphila* is currently the best indication of cladistic relationship, we do not attribute great weight to this relationship largely because only two synapomorphies (characters 2 and 4) were found to support this sister-group relationship.

The two basal lineages within *Lemnaphila* are first *L. longicera*, which is the sister lineage to the remaining species in the genus, followed by *L. scotlandae*. The next four species, which are all Neotropical in distribution (often at the same habitat), are obviously closely related and are very similar externally, and in the four equally parsimonious trees, these four species varied in position with respect to each other. In two of these trees, *L. wirthi* was basal to the other three, and in the other two trees, *L. grossoae* was the basal lineage. The single tree from successive weighing, howev-

Table 3. Status (i.e., nonadditive –; inactive J) and weights of characters after successive weighing.

Character No.	1	2	3	4	5	6	7	8	9	10	11	12
Weight, status	10– [	10+ [	10+ [	10– [	10+]	10+]	10+ [	10– [	10+]	2+ [	10– [	10+ [
Character No.	13	14	15	16	17	18	19	20	21	22	23	24
Weight, status	10+ [	10– [	10+ [	0+ [	10+ [	10– [	10+ [	10– [	10+ [	10+ [	10+ [	10+ [

er, has *L. wirthi* as the basal lineage with the other three species forming an unresolved trichotomy (Fig. 27).

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